

## THE STATUS OF THE RHODOPIDAE (GASTROPODA: EUTHYNEURA)

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### ABSTRACT

Based on investigations of *Rhodope veranii*, *R. transtrosa* sp. nov. and *Helminthope psammobionta* gen. et sp. nov., the organization of the Rhodopidae is reconsidered. *Helminthope* is characterized by a slender body, by typical verrucose rods, by lack of a radula, stomach and dorso-rostral caecum, and especially by five free ganglia on the visceral loop. The animals inhabit the interstia of subtidal sands. The number of ganglia confirms earlier developmental investigations in *R. veranii* with respect to the pentaganglionate (= euthyneurous) level. The shift of the visceral ganglion to the left side, as well as the lack of special vacuolar bodies in the epidermal cells, argue against a classification of the Rhodopidae within the Anthobranchia (= Doridacea) and the Nudibranchia. The lack of both a paired procerebrum and cerebral gland excludes a direct relationship of the Rhodopidae with the Gymnomorpha (Onchidiacea, Soleolifera) and Pulmonata. Furthermore, the free visceral ganglion in *Helminthope* and the monaully preclude a classification of the Rhodopidae amidst higher tectibranch groups (= Paratectibranchia). Consequently, the Rhodopidae, (including *Helminthope* and five presumed species of *Rhodope*) remain as a taxon Rhodopomorpha, of uncertain systematic rank and affinity, as a specialized off-shoot from the lower opisthobranchs.

### INTRODUCTION

At the present time, the Rhodopidae are scientifically known only by the Mediterranean *Rhodope veranii* Kölliker and by the southwest Atlantic *R. marcusii* (see p. 308). Since the original description of *R. veranii* (Kölliker, 1847), few additional specimens have been found. Due to the investigations of Graff (1883), Böhmig (1983), and Riedl (1959, 1960), however, we are fairly well informed about the anatomy, histology, biology, and development of this species; Marcus & Marcus (1952) supplemented this knowledge by the description of a closely related form (see p. 308). The central question about *Rhodope* concerns its phylogenetic affinities. After the definitive classification of the species as an euthyneurous gastropod (Riedl, 1960), its affinities within that subclass still remain uncertain (cf. Oberzeller, 1969; Salvini-Plawen, 1970; Tillier, 1984: 359). Further recent findings of *Rhodope veranii*, *R. transtrosa*, and *Helminthope psammobionta* enlarge our knowledge of the Rhodopidae and permit a re-evaluation of its systematic relationships.

#### *Rhodope veranii* Kölliker

Fifteen *Rhodope veranii* were recently found in one of the marine aquaria of the Zoo-

logical Institute (Universität Wien) filled with sediment and secondary hard-bottom material from the Northern Adriatic Sea and the Gulf of Naples. In nature, *R. veranii* appears to inhabit shallow subtidal areas with stones and *Ulva* growth (Graff, 1883: p.74; F Star-mühlner, pers. comm., for Rovigno/Istria; Salvini-Plawen in Arnaud et al., 1986: p 158). All specimens beyond 1 mm in length are characterised by the more or less distinctly T-shaped dorsal orange-red pigmentation (Riedl, 1960). In contrast to previously found animals with a maximum length of 4 mm (Graff, 1883: p.74; Riedl, 1960: p.297), the present individuals were distinctly larger, ranging up to 8 mm in length. The subepithelial spicules and the inconspicuous eyes are typical. However, there is remarkable variation in the location of the genital opening: Graff (1883: p.79) confused the protonephridiopore with the male gonopore and the anus with the female opening (both located at the right posterior border of the transverse pigment bar, i.e. anterior to the middle of the body). Riedl (1959: his Fig. 2) located the genital opening at the right anterior border of the transverse pigment bar, irrespective of the state of contraction of the animals. Apparently the location of the gonopore varies in different individuals. The examination of six serially sectioned specimens (Riedl's and the present material) revealed that only one specimen possessed the genital

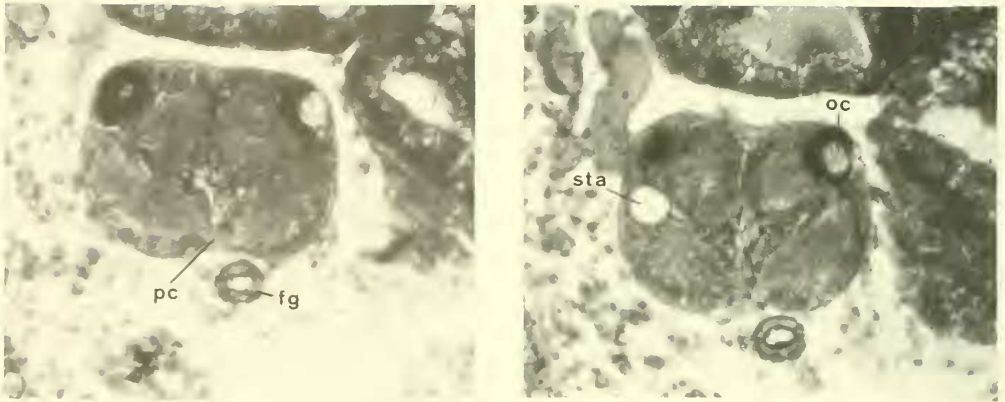


FIG. 1. *Rhodope veranii*: Two successive cross sections through the cerebral nervous ring in a specimen with the foregut (fg) outside the pedal commissure (pc). oc eye, sta statocyst.

opening in the location indicated by Riedl; two animals show the gonopore laterally at the level of the perioesophageal central nervous mass (with embedded eyes visible, see Fig. 1), while three individuals show the genital opening distinctly anterior to the ganglia complex, viz. anterior to the eyes (in one the gonopore is even located at the level of the mouth).

In the concentrated nervous system the closely adjoining cerebro-pleuro-parieto-intestinal ganglia (cf. Riedl, 1960; Oberzeller, 1969) have a short cerebral commissure and the eyes as well as optical ganglia incorporated (Fig. 1); the optical connective itself has its origin in the pleuropedal connective. Besides the buccal connectives, there are three pairs of rostral nerves, the two medial ones with a common (?) root running to the oral region (labial nerves). The most lateral one at each side corresponds to the Hancock's or rhinophoral nerve in other opisthobranchs and has a basal swelling which shows a double root in the cerebral ganglion; there is no head-shield-tentacle nerve (Huber, 1987). In addition, a strong lateral nerve, with bifurcated root in both the (cerebro-) pleural ganglion and the pedal ganglion, runs anterior-laterally to the body flanks; at the right it also innervates the copulatory organ. The two abdominal 'nerves' (right-visceral and left-genital) running ventrally close to the body end are regularly provided with nuclei, thus assuming the aspect of weak medullary cords. A peculiarity was noticed in one of the specimens: instead of being surrounded by the mass of the concentrated ganglia, the oe-

sophagus runs outside (i.e. below) the pedal commissure (Fig. 1).

The midgut shows the usual, somewhat winding, rostral caecum or right midgut gland (Riedl, 1960: p. 284). Close to the junction of the short intestine and the voluminous midgut there is a narrow pouch or small diverticulum. In both Riedl's and the present material, this pouch is lined with a low, ciliated epithelium that is histologically continuous with the intestinal epithelium. In contrast to Böhmig (1893: p.56 & Fig. 13), however, this pouch is well separated from the adjacent intestine, and, in agreement with Riedl (1960: pp.284–285), it corresponds to the remnant of the true stomach.

The chromosome number of *R. veranii* is  $2n = 32$  (pers. comm. Claudia R. Schweizer, Wien). The spermatozoa, with a spiraled head, have a characteristic shape and fine structure; in some aspects they appear to be fairly primitive and similar to prosobranch sperm (pers. comm. F. Giusti di Massa, Siena).

#### *Rhodope transtrosa* sp. nov.

A single specimen (Fig. 2A) was collected from an aquarium (Ehrmann Zoo, Wien XII) filled with phytal material from the tropical Indo-Pacific (Ceylon/Sri Lanka ?). The living animal measured 1.65 mm x 160  $\mu$ m maximum. The anterior third of its whitish body is provided with a characteristic dorsal transverse bar (*transtrum*) of orange-reddish pigmentation (about 160  $\mu$ m in length). The anteriormost section is markedly elongated and

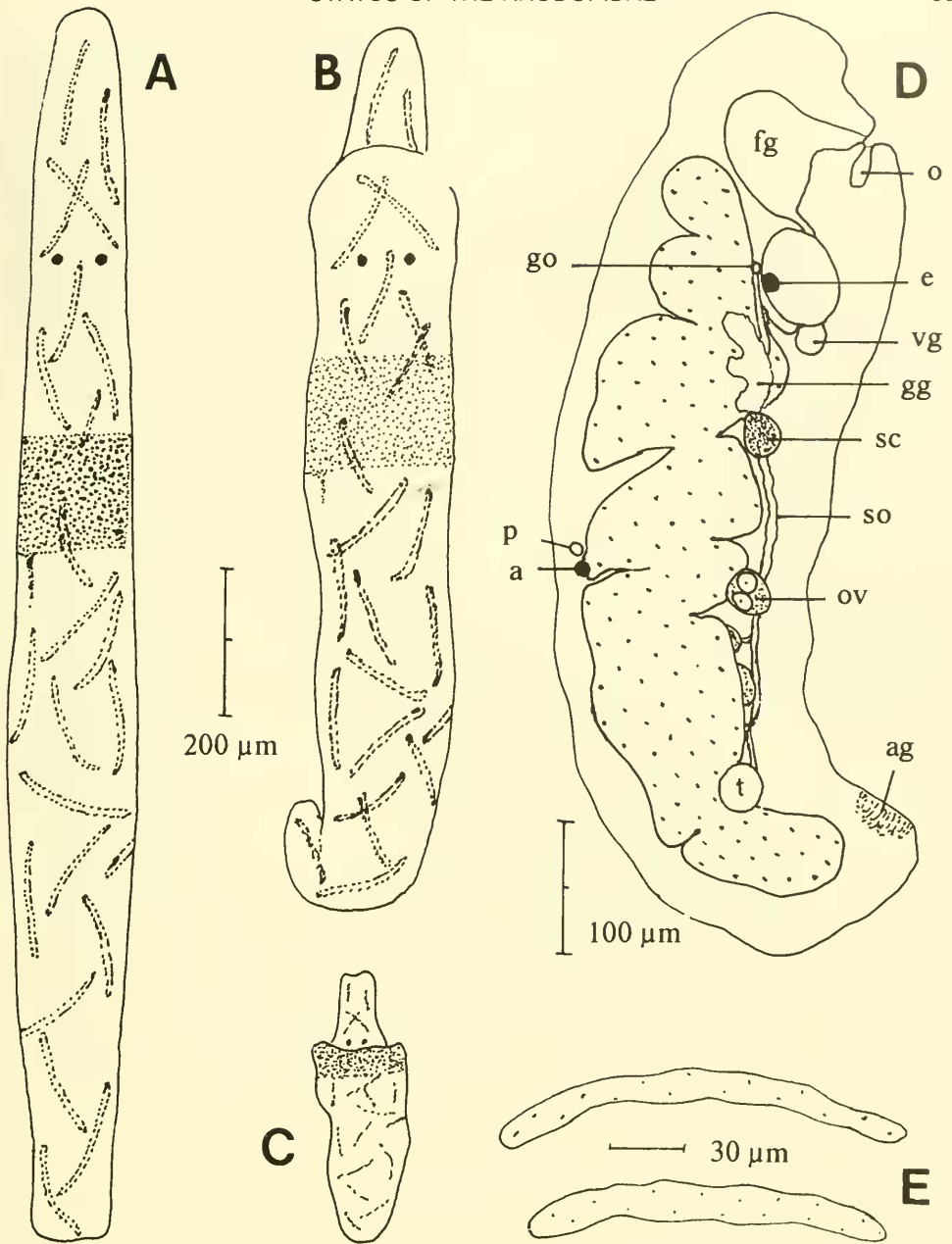


FIG. 2. *Rhodope transtrosa*: A: living animal (1.65 mm); B: semi-preserved animal; C: contracted animal; D: arrangement of organs as seen from the right side in preserved animal; E: spicules. a anus, ag adhesive gland, e eye, fg foregut, gg genital gland, go genital opening, o outlet of oral glands, ov ovarian sac, p protonephridiopore, sc spermatocyst, so hermaphroditic duct, t testicle, vg visceral ganglion.

acts as a highly-bendable snout with subfrontal mouth opening; in the contracted state this snout may be retracted far into the subsequent, still pre-ocular section. The eyes are

clearly visible in life. The body is somewhat truncated terminally due to the distinct adhesive organ. The spicules are fairly densely arranged and are slightly curved with a faintly

verrucose surface. They measure 150–170  $\mu\text{m}$   $\times$  14–17  $\mu\text{m}$  (Fig. 2E).

The internal organization closely resembles that of *R. veranii*, but there are some distinct differences. Ventral to the subterminal mouth, a short median sac bearing the peripherally arranged oral glands opens (the glands are arranged as a paired cluster in *R. veranii* and *R. marcusii*). The foregut shows a precerebral enlargement with taller epithelium, but no pharyngeal bulb. This section receives the salivary glands in paired arrangement. Immediately behind the central nervous complex the foregut leads dorsally into the sac-like midgut (midgut-gland). The latter forms an elongated organ extending from above the foregut to the posterior end of the body; in the preserved animal, there are several contraction-folds along its course, but no actual winding. Somewhat behind the mid-length of the body, the short intestine emerges dorsally from the sac-like midgut and runs directly, without any winding, to the right. It opens laterodorsally closely behind the laterodorsal protonephridiopore, both being located (in contrast to *R. veranii* and *R. marcusii*) posterior to the middle of the body (preserved animal). Immediately adjacent, and to the left of the intestine, a small but distinct posteriorly directed pouch or diverticulum is present; this corresponds to the remnant of the true stomach in *R. veranii*.

The nervous system largely resembles that of *R. veranii* with respect to the general arrangement of the ganglia and, on each side, the two proximally joined labial nerves, the double root of the rhinophoral nerve, the bifurcated (pleural and pedal) root of the lateral nerve, and the optical ganglion emerging with its connective from the pleuropedal connective. Differences are evident in the less concentrated state of the ganglia with the discrete statocysts between the cerebro-pleuroparieto-intestinal ganglia and the pedal ganglia, the discrete optic ganglia, the strong parapedal commissure, the fairly free and median visceral ganglion, as well as the symmetrical origin of the right visceral and left genital medullary nerves (cf. Huber, 1987).

In the hermaphroditic genital system there is a 55  $\times$  45  $\mu\text{m}$  terminal testicle and a much larger testicle (70  $\times$  50  $\mu\text{m}$ ) more anteriorly on the left. The median hermaphroditic duct then connects two ovarian sacs on the left, one on the right, and two more on the left (these being located anterior to the anal region of the body). Approximately half way between the

intestine and the central ganglia complex the spermatheca turns to the right and continues in the form of a narrow connection with an enlarged portion filled with sperm. In contrast to *R. veranii* and more similar to *R. marcusii*, this sac represents a distinct elaboration (spermatheca) rather than a simple enlargement of the spermatheca (as in *R. veranii*). It opens anteriorly into a three-lobed glandular complex (albumen and mucus glands) from which the genital duct runs antero-laterally to open on the right at the level of the cerebral ganglia and eyes. In contrast to *R. veranii* and *R. marcusii*, no copulatory organ is developed in the present specimen.

### *Helminthope psammobionta* gen. et sp. nov.

This mesopsammic species comes from the western North Atlantic. Specimens were collected by R. Rieger (Innsbruck) and W. Sterrer (Bermuda) from Bermuda (North Rock reef and Tobacco Bay, at 8–10 m depth), North Carolina (30 m depth) and Georgia (2 m depth). They inhabit fairly clean, coarse subtidal sands (cf. Rieger & Sterrer, 1975: pp. 263–264 & their Figs. 34–35). The present animals ranged between 1 mm and about 2.5 mm in length (Figs. 3–4) and are circular in cross section (diameter 60–150  $\mu\text{m}$ ), but are able to contract by 30–50%. They are whitish with black eyes; in transmitted light they appear transparent-colourless with a darker, somewhat greenish tinge to the midgut. The body openings are almost invisible as two ciliated patches arranged one close behind the other on the right anterior side. These patches indicate the sites of the protonephridiopore and the anus. The genital opening could not be seen. Because of its internal organization (below), the present specimens are defined as *Helminthope psammobionta* gen. et sp. nov. (Figs. 3–4).

All three specimens sectioned were unfortunately poorly preserved for histological examination, so only an outline of the body organization can be given. The entire body is covered by ciliated epidermal cells among which gland cells are interspersed. In no animal could a definite terminal gland be seen (in contrast to *Rhodope veranii*, *R. marcusii* and *R. transtrosa*; see Fig. 2D). The loosely and irregularly arranged spicules measure between 45  $\times$  5.5  $\mu\text{m}$  and 70  $\times$  7  $\mu\text{m}$ , and they are weakly curved to slightly angled or geniculate in shape (Fig. 4C). Towards their tips the spicular surface is generally roughened,

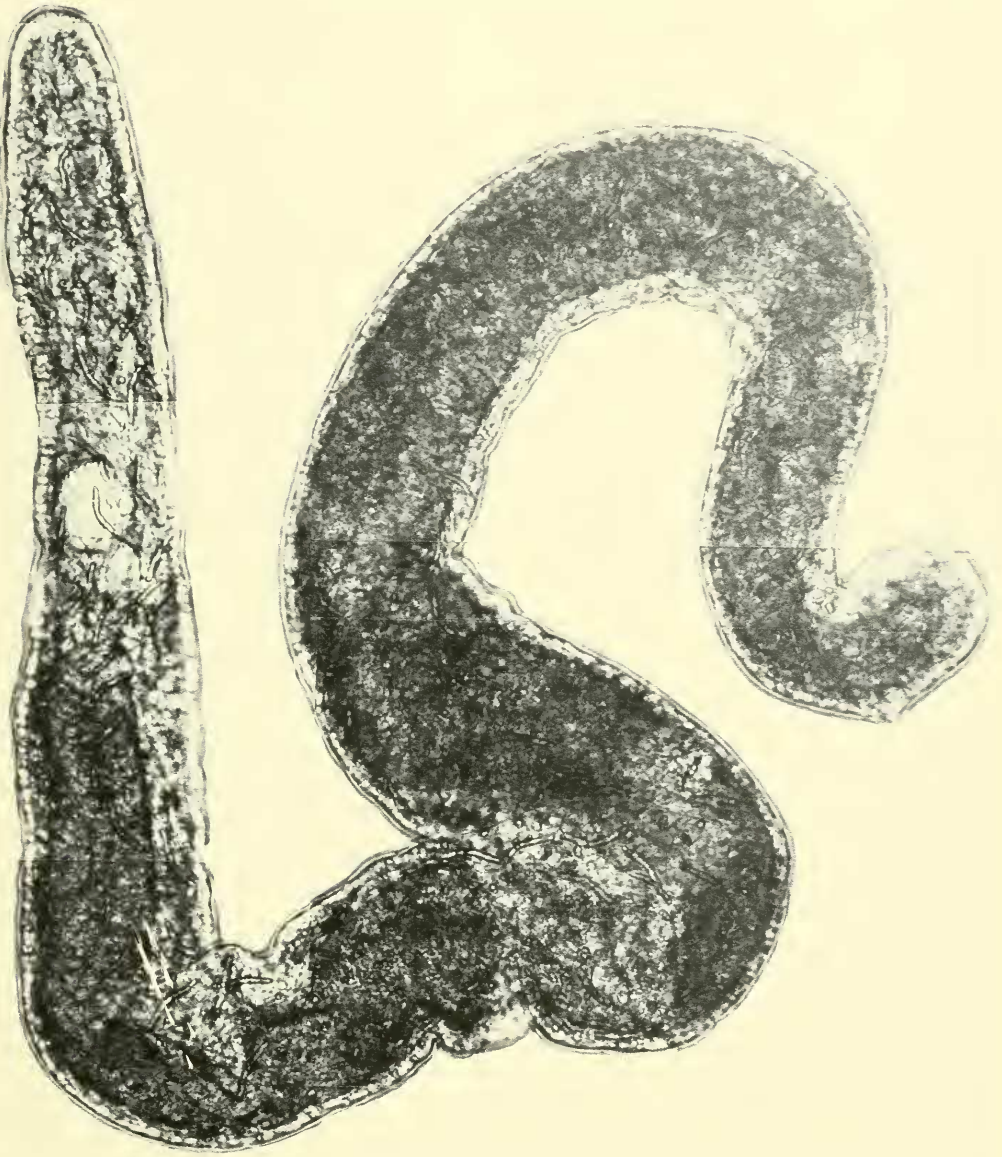


FIG. 3. *Helminthope psammobionta*: living specimen (about 1.5 mm in size) from Bermuda.

and some spicules seem to be hollow (Rieger & Sterrer, 1975: Fig. 34). The spicules are situated in the fibrous connective tissue directly below the epidermis and are surrounded by a spicule-forming cell (Rieger & Sterrer, 1975: Fig. 35). In addition to the elongate spicules (similar to those in *R. veranii* (Graff, 1883: p.75-76) or *R. transtrosa* (Fig. 2E)) very small and platelet-like elements are embedded subepithelially. As indicated by the

high contractility of the body, there is a well-defined longitudinal musculature; no regular circular fibres could be seen.

The alimentary canal begins with a subterminal mouth. This leads into a narrow foregut which soon widens and is lined with a tall ciliated epithelium surrounded by circular muscle fibres (pharynx). A pair of ill-defined salivary glands accompany the foregut dorsolaterally. In the region of the cerebral ner-

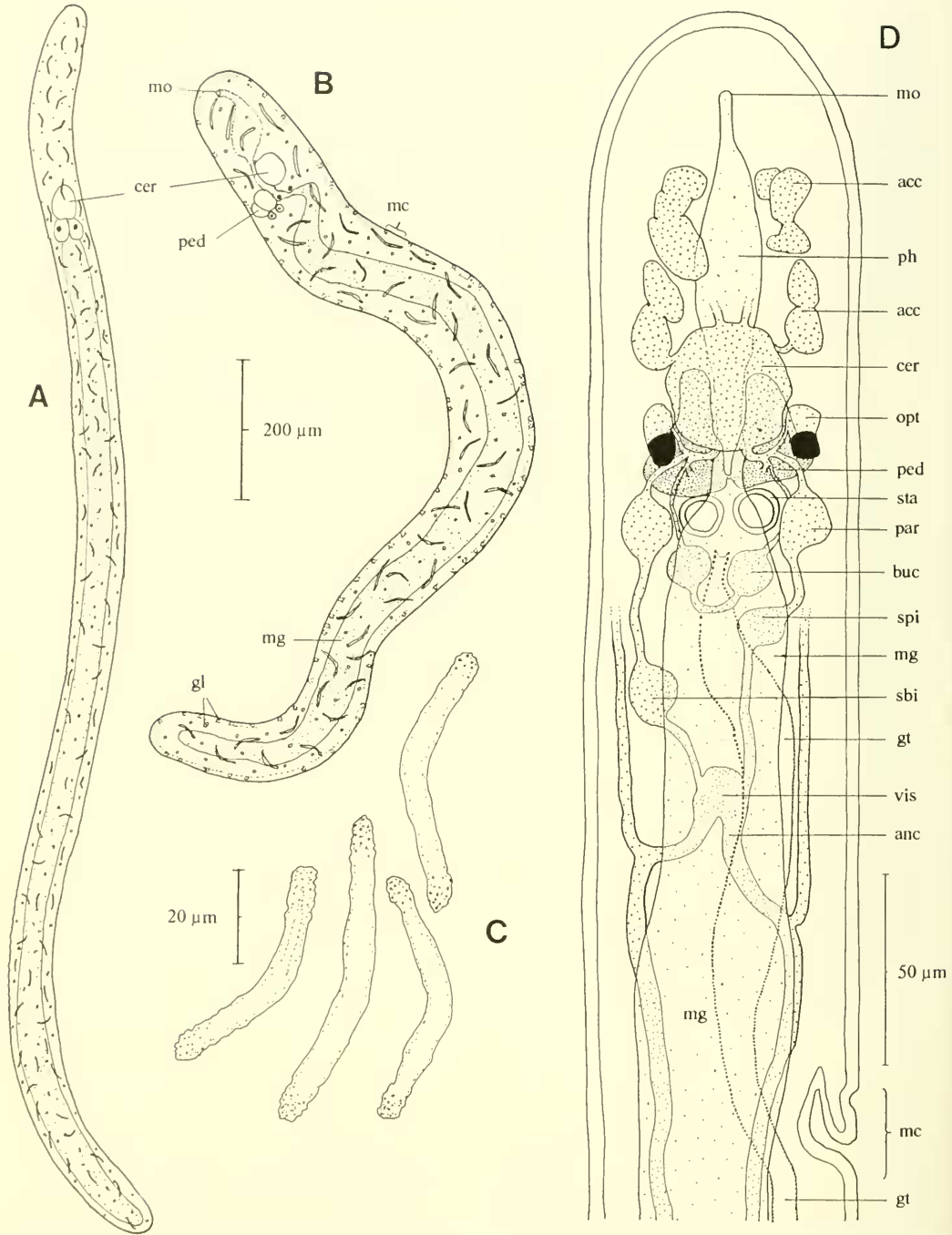


FIG. 4. *Helminthope psammobionta*: specimen from North Carolina gliding (A) and in contracted state below cover glass (B); C: spicules; D: main internal organization. acc accessory ganglia, anc right abdominal nerve cord (= visceral nerve), buc buccal ganglion, cer cerebro-pleural ganglion, gl epidermal glands, gt genital tube (spermoviduct), mc area of (reduced) mantle cavity, mg midgut, mo mouth opening, opt optic ganglion, par parietal ganglion, ped pedal ganglion, ph pharynx, sbi sub-intestinal ganglion, spi supra-intestinal ganglion, sta statocyst, vis visceral ganglion.

vous ring the foregut narrows again. Behind the pedal ganglia the oesophagus connects to the midgut. There is no antero-dorsal caecum (right digestive gland). The midgut represents a homogeneous tube-like organ with high glandular epithelium extending the length of the body. There is no histological break during the course of the midgut except for the almost total disappearance of the lumen in the terminal portion (representing the posterior = left midgut gland?). The lumen is also restricted to a somewhat narrower space posteriorly due to the genital organs. The intestine emerges from the midgut dorsolaterally (approximately 100  $\mu\text{m}$  behind the visceral ganglion) and runs obliquely direct to the lateral anus. Only in one specimen could an organ closely associated with the anus and extending a short distance anteriorly be discerned, probably the protonephridium.

In the nervous system apart from the cerebro-pleural complex all ganglia are separate (Fig. 4D). The fused cerebro-pleural ganglia still show a mid-dorsal incisure and a distinct cerebral commissure; the pleural portion is separated by an accumulation of nuclei. Anteriorly, at least two pairs of cerebral nerves (the labial and the Hancock's/rhinophoral) leave the ganglia. Very characteristic is the presence at each side of two complexes of accessory ganglia. These appear to be incorporated in the course of the cerebral nerves, each complex assuming two to three swellings.

A short connective runs from each cerebral ganglion to the respective pedal ganglion and a strong, terminal cerebropleural connective splits to connect with the optic, the parietal, and the pedal ganglion, as well as the buccal ganglion at each side. The buccal ganglia themselves are well separated and lie behind the statocysts. The small optic ganglia with the embedded eyes are separate from the cerebral ganglia and are located above the pedal ganglia (Figs. 4A,D). Each of the latter is very prominent and shows an anterior lobe. A lateral nerve of the pedal ganglion emerges at each side close to the pleuropedal connective. The statocysts, each with a single statolith, are close by, but they are separate from the ganglia and main nerves. The parietal ganglia are widely separated from the cerebral complex. On the right a strong connection exists to the supra-intestinal ganglion lateroventrally to the midgut, and to the left a much longer connective leads to the (ventro)

lateral sub-intestinal ganglion. Both connectives unite in the mid-ventral visceral or abdominal ganglion, which appears to be located at a fairly constant distance of about 135  $\mu\text{m}$  from the beginning of the cerebral ganglia. In histological continuation of the right (supra-intestinal) connective the strong genital 'nerve' emerges from the left portion of the ganglion and runs posteriorly as the left cord, and the left connective continues into the right cord (visceral nerve). Thus, there is a chiasma of fibres in the visceral/abdominal ganglion reflecting the only remaining trace of streptoneury. Furthermore, both abdominal 'nerves' terminate together with the midgut-sac and exhibit a regular coat of nuclei. They thus assume the aspect of medullary cords and each gives off a strong anterior branch (Fig. 4D).

The genital system is absent in one specimen, is represented only by the rudiment of a simple tube extending below the midgut in a second specimen, and is not fully differentiated in the third sectioned individual. In the latter two individuals, the anteriormost part of the genital system is represented by a narrow tube extending posteriorly from between the buccal ganglia; the outer portion and genital opening could not be discerned and still appear to be absent. The genital tube (spermoviduct) gradually enlarges posteriorly where it is lined with a high, glandular epithelium without a well-defined lumen (prostate gland?). The tube then continues posteriorly between the midgut and nervous system, its epithelium decreasing again in size toward the anal region. More posteriorly, approximately 850  $\mu\text{m}$  from the anterior tip of the body (about 600  $\mu\text{m}$  behind the visceral ganglion or 500  $\mu\text{m}$  behind the anal region), the simple tube enlarges again to become a weakly ciliated vesicle filled with spermatozoa (spermatheca). This vesicle opens dorsally with its terminal narrowed portion into a voluminous (albumen and mucus) gland, the anterior region of which is lined by densely granulated and ciliated cells which are then replaced posteriorly by large slime cells. A narrow, ciliated duct continues from this gland and appears to become a ramified germ gland. This latter condition could not, however, be ascertained in detail, and only some accumulation of sperm in vesicles (testicles) were observed. Thus, as is *Rhodope veranii* (Riedl, 1960:p.299), the present new species also appears to be protandric (gonochorism is also possible).

### Systematic Discussion of the Rhodopidae

In contrast to *Rhodope veranii*, *R. transtrosa* and *R. marcusii* (see pp. 300, 302), the new type *Helminthope psammobionta* is characterized and defined by the wide nervous system with free ganglia and the differentiation of precerebral (= accessory) ganglia, by the axial connection of the foregut and midgut without anterior caecum, and by the lack of a ventroterminal adhesive gland. These characteristics indicate that it belongs to a distinct genus. It is also characterized by the elongate body without pigmentation, the less verrucose and smaller spicules, the far posterior location of the spermatheca and the presence of the albumen/mucus genital gland behind it, as well as the interstitial habitat. There is, however, no doubt that *Helminthope* is a rhodopid characterized by a pentaganglionate visceral loop with medullary visceral and genital nerves, subepidermal spicules, reduced mantle cavity on the right side (anus and protonephridiopore), lack of a shell, radula, jaws, stomach, heart, and head-shield/tentacles.

The systematic roundabout of the Rhodopidae is summarized in Riedl (1959). With respect to the developmental characters and the pentaganglionate visceral loop, the family definitely belongs to the Pentaganglionata = Euthyneura (Riedl, 1960: pp.303–312; Salvini-Plawen, 1970; Haszprunar, 1985). A more precise classification has assumed a close affinity to the Soleolifera and Onchidiacea with the inclusion of all three groups within a separate euthyneuran subclass Gymnomorpha (cf. Riedl, 1960; Oberzeller, 1959; Salvini-Plawen, 1970; Arnaud et al., 1986). Such a classification cannot, however, be upheld because the present investigations demonstrate that neither *Rhodope* nor *Helminthope* possess a procerebrum and/or cerebral glands. This special neurosecretory/neurohaemal system is characteristic of the Pulmonata and Gymnomorpha (cf. Haszprunar, 1985). In addition, both groups (= clade of Aeropneusta) are characterized by the absence of a postero-lateral cerebral nerve equivalent to the Hancock's or rhinophoral nerve present in Rhodopidae as in all other opisthobranchs (Huber, 1987). Thus, the Rhodopidae cannot be included within one of these two supra-orders (Fig. 5). On the other hand, the slug *Smeagol manneringi* (Climo, 1980), which due to the (inaccurate) original description had been excluded from the Gymnomorpha (Haszprunar, 1985; Arnaud et al.,

1986), in fact belongs to the supra-order Gymnomorpha: a re-examination has revealed the presence of a procerebrum and of cerebral glands which, together with other characters, place the species in closer affinity to the Onchidiidae (pers. comm. G Haszprunar; cf. Arnaud et al., 1986: p.175).

An ultrastructural investigation of the integument of *Rhodope veranii* (pers. obs.) and *Helminthope* (Rieger & Sterrer, 1975: their Fig. 35) demonstrates that there are no special vacuolar cells provided with vesicles (amphidisk-like inclusion; cf. Schmekel, 1982,1985) and consequently the Rhodopidae cannot be classified within the Nudibranchia s.s. (= less Doridacea). Because, on the other hand, investigated members of *Pseudovermis* (Aeolidacea: Heteroprocta) possess vacuolar cells (pers. obs.), their lack in Rhodopidae could perhaps be correlated with the diminutive size (as accessory ganglia appear to be) or the special habitat. An identical argument would be valid with respect to the Anthobranchia (= Doridacea or Holohepatica or '(Eu-)Ctenidiacea') which have special vacuolar cells in the rhinophores (cf. Kress, 1981; Schmekel, 1985); because, however, all tentacles are reduced in the Rhodopidae no comparison is possible here.

Up to the present, the configuration of the nervous system provided a valid argument to exclude *Rhodope* from the Anthobranchia (as well as from Pleurobranchomorpha and Nudibranchia s.s.; cf. Salvini-Plawen, 1970). The presence of the visceral/abdominal ganglion in *Rhodope veranii* on the left side, or almost fused with the sub-intestinal ganglion (Riedl, 1960; Oberzeller, 1969), is the opposite of the condition found in the Eleutherobranchia (Pleurobranchomorpha, Anthobranchia and Nudibranchia; cf. Haszprunar, 1985). Against this argument, however, the more conservative configuration in *Helminthope* (Fig. 4) and even in *R. transtrosa* still makes any concentration possible. This is a renewed confirmation that the position of the visceral ganglion on the left side is a convergence. On the other hand, the visceral ganglion in Bullomorpha, Aplysiomorpha = Anaspidea, and Saccoglossa (except the Cylindrobullidae, cf. Burn, 1966), as well as in Umbraculomorpha, Acochliomorpha, and Gymnosomata, is already fused to the left side (generally with the sub-intestinal ganglion). Because *R. transtrosa* and *Helminthope* show a well-separated visceral ganglion, no link can be proposed among these more advanced tecti-



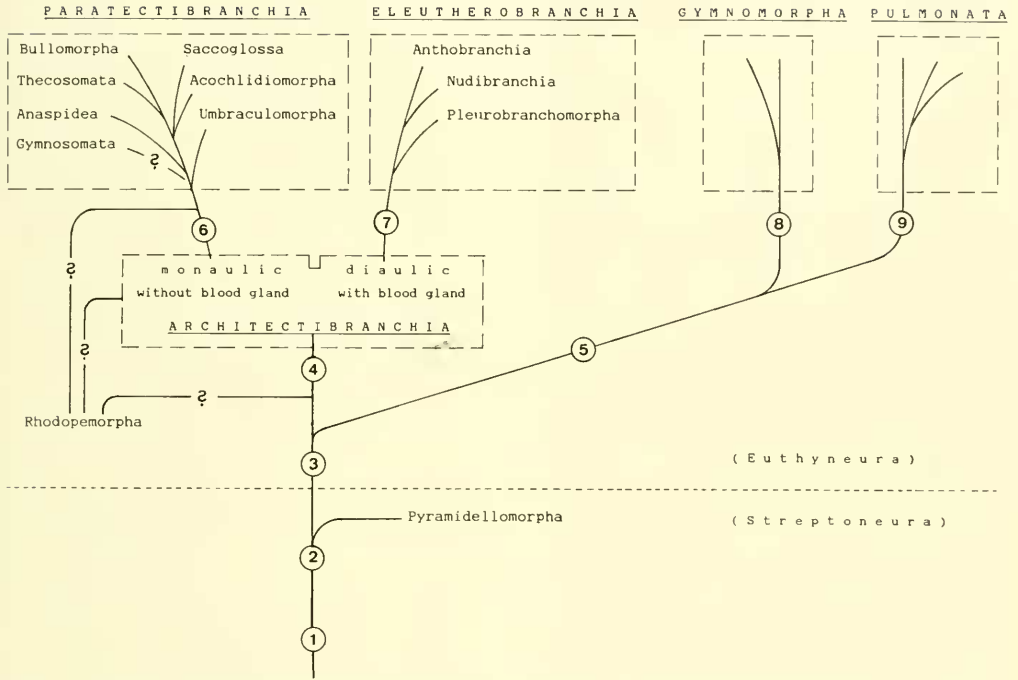


FIG. 5. Relationship of Rhodopemorpha within pentaganglionate (= euthyneurous) gastropods: 1 = Streptoneura with epiathroid nervous system, tentacle nerves bifurcated, parapedal commissure; heterostrophy; mantle cavity with two opposed ciliary tracts and devoid of ctenidia; eggs united by chalazae, spiral type of sperm with glycogen helices within midpiece. 2 = Eyes median of tentacles; cerebral ganglia with giant cells, pedal ganglia with lateral nerve; with paired rhinophoral (= Hancock's) nerve; small animals with reduction of paired oralis nerve. 3 = Elongation of head-pedal complex with parietal ganglia; with pallial caecum and repugnatorial glands. 4 = Opisthobranchia: Head-shield with bifurcated tentacle (= clypeo-capitis) nerves; Hancock's sense organs with external branch of labiotentacularis nerve. 5 = Procerebrum with cerebral glands and dorsal bodies; small animals (= without oralis nerves), anterior shift of female genital opening outside the mantle cavity and restriction of the opening of mantle cavity: Aeropneusta; loss of paired rhinophoral nerve. 6 = Anterior gizzard. 7 = Disintegration of head-shield; visceral ganglion migrates to the right side to fuse primarily with the supra-intestinal ganglion; chromosomes restricted to generally 12-13 pairs. 8 = Mantle cavity reduced to 'cloaca', or lost; loss of shell, pedunculated eyes. 9 = Mantle cavity becomes a 'lung'.

branches (= Paratectibranchia, below). Finally, the bifurcated lateral nerve in *Rhodope* (see pp. 300 and 302) has a similar origin in several Nudibranchia. However, because it corresponds to the purely latero-pedal nerve in *Helminthope* and other Euthyneura (Huber, 1987; see Fig. 5), this similarity between *Rhodope* and those nudibranchs appears to be convergent due to concentration.

Whereas the structure of the spermatozoa gives little evidence of phylogenetic value

(see p. 300), the chromosome number in *Rhodope veranii* with  $n=16$  appears to be of more interest. The general chromosome numbers in Eleutherobranchia are  $n=12$  (Pleurobranchomorpha) or  $n=13$  (Anthobranchia and Nudibranchia), in Saccoglossa  $n=17$  (except for *Bosellia* :  $n=7$ ), and in other Tectibranchia likewise  $n=17$  (see Burch, 1967; Schmekel, 1985; Vitturi et al., 1985). Exceptions (so far as known) include the cephalaspideans *Scaphander*, *Hami-*

*noea*, *Philine aperta* and two Smaragdinelidae with  $n=18$ , *Philinoglossa* with  $n=13$ , the anthobranch *Platydoris* with  $n=12$ , two *Aplysia* species (Anaspidea) with  $n=16$ , as well as the dendronotacean nudibranch *Tethys leporina* with  $n=16$  (see Curini-Galletti, 1985; Vitturi et al., 1985). These two latter exceptions, as well as the chromosome number  $n=16$  in *Veronicella* (Gymnomorpha) and the lower pulmonates *Siphonaria* and *Bakerilymnaea* (cf. Burch, 1967), are of special interest since they demonstrate a polyphyletic decrease of the chromosome number  $n=17$  along with anagenesis (in higher pulmonates, the number of chromosomes is generally increased; cf. Burch, 1967). Thus, the number  $n=16$  in *Rhodope* appears to show that the Rhodopidae cannot be directly linked with one of the present orders, but rather it demonstrates the primitive level still reflected in some Anaspidea, Nudibranchia, Gymnomorpha, and lower Pulmonata.

The monaully in the genital apparatus of *Helminthope* as well as of *Rhodope* (though with possible incipient functional diauly in *R. veranii*; cf. Böhmig, 1893: p.81) excludes a closer relationship to the dialucic Eleutherobranchia, Sacoglossa, and Anaspidea (see Fig. 5). In addition, it is interesting to note that the gonad includes separate testicles and ovaria, a condition only known in several Streptoneura.

In conclusion, the pentaganglionate Rhodopidae cannot, on the one hand, be directly linked with Gymnomorpha and Pulmonata, nor, on the other hand, can they be classified within the Eleutherobranchia (Pleurobranchomorpha, Anthobranchia, and Nudibranchia), Saccoglossa, or Anaspidea. The Rhodopidae share only a general level of organization with several tectibranch gastropods. According to a recent analysis by Haszprunar (1985), however, the tectibranchs should be subdivided into the conservative group of Architectibranchia (Diaphanoidea, Ringiculoidea, Acteonoidea) and the other more advanced tectibranchs (Fig. 5); this latter group preferably should be named Paratectibranchia (Salvini-Plawen, 1988), and are monophyletically characterized by a gizzard (if not secondarily reduced). Since the two proximally joined labial nerves on each side in *Rhodope* (according to Huber 1987) correspond to the internal plus external branch of the labiotentacularis nerve, such condition would the Rhodopidae unequivocally classify within the opisthobranchs (i.e. above the level 4 in

Fig. 5). At the present time, the characters of the Rhodopidae only permit this family to be classified as a taxon **Rhodopomorpha** nov. of uncertain systematic rank representing a highly specialized offshoot of the lower opisthobranchs (Fig. 5).

Recent Rhodopomorpha, with at present the single family Rhodopidae, include the following three phytal and three interstitial members (cf. Rieger & Sterrer, 1975: p.262–265; Arnaud et al., 1986: p.158,171):

1. *Rhodope veranii* Kölliker, 1847, from the Adriatic Sea and the adjacent Mediterranean, measures 1–8 mm and inhabits shallow subtidal areas with stones and *Ulva*. It is characterized by an orange-red, roughly T-shaped dorsal pigmentation as well as by verrucose and more pointed, slightly bent spicules of 90–200  $\mu\text{m}$  length. Reduced mantle cavity anterior to the middle of the body.

2. *Rhodope marcusi* sp. nov. (= *R. veranii* Marcus & Marcus, 1952, nec Kölliker, 1847; = *Rhodope* species A in Arnaud et al., 1986: p.158) comes from the Bay of Santos (Brazil, off São Paulo) and lives in the rocky or stony tidal zone among *Sargassum stenophyllum* and *Padina*. In contrast to *R. veranii* Kölliker, and to *R. transtrosa* (below), the c. 2 mm long specimens are characterized by the lack of orange-red pigmentation, by the crescent shaped spicules, and by the position of the reduced mantle cavity with anus and protonephridiopore in the mid-length of the body (cf. Marcus & Marcus, 1952).

3. *Rhodope transtrosa* sp. nov. is at present known only by a single specimen from an aquarium filled with phytal material from tropical Indo-Pacific waters. It is characterized by an orange-red transverse bar at the anterior third of the 1.65 mm long and slender body, as well as by scarcely verrucose, slightly curved spicules of 150–170 x 14–17  $\mu\text{m}$  size. The reduced mantle cavity is located somewhat posterior to the middle of the body; differences in the internal characters are as indicated above. Type: Naturhistorisches Museum, Wien, No. 83438.

4. *Rhodope* species D was recorded from coarse shell-sand at 25 m off Bergen, Norway by Karling (1966). This colourless specimen is 1.5 mm long and accordingly should already possess the reddish T-pigmentation if conspecific with *R. veranii*. It is possibly conspecific with the specimens found in shell-sand at 50 m by Swedmark (1958: p.61) and off Madeira by Langerhans (in Graff, 1883: p.74–75). This eastern Atlantic species pos-

sesses slightly curved verrucose rods (65–100  $\mu\text{m}$ ) and pointed spicules similar to *R. veranii*, as well as ramified elements (cf. Karling, 1966).

5. *Rhodope* (?) *crucispiculata* sp. nov. (= *Rhodope* species C in Arnaud et al., 1986) was collected by Christine Schöpfer-Sterrer from subtidal sand at 14 m from the coast of Tunisia (cf. Rieger & Sterrer, 1975: p.262, 265). Though certainly immature (400  $\mu\text{m}$  in size), this species is defined and easily recognizable by the densely arranged, regularly cross-shaped spicules (25–60  $\mu\text{m}$ ) with central hole.

6. *Helminthope psammobionta* gen. et sp. nov. (= *Rhodope* species B in Arnaud et al., 1986). The new genus and species is characterized as described above. Type: Naturhistorisches Museum, Wien, No. 83439.

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